to the freshwater source), and (2), other microhabitat characteristics such as topography or ground cover did not differ markedly from the other transects.

Investigating algal diversity in the mangrove would also be valuable because lower herbivory pressure may result in greater overall algal species diversity (Taylor et al. 1986). Moderate herbivory has been shown to create a type of intermediate disturbance, preventing otherwise dominant species from excluding slower-growing, less-dominant species (Connell 1970, Taylor et al. 1986). In addition, if the mangrove is a refuge habitat, a reciprocal transplant experiment involving algae from both inside and outside the mangrove area could test the hypothesis that the selection for secondary metabolite production may be influenced by herbivory regimes. If algae with high concentrations of secondary metabolites are favored in areas with greater herbivore pressure, we would expect algae from the mangrove to exhibit fewer chemical defenses than algae from habitats with greater herbivory.

In conclusion, our bioassay suggests that the mangrove area may provide a refuge habitat from herbivory, but further study is needed to resolve this question. If the area is a refuge, it raises many possible questions about algal diversity and physiology that may be easily tested in future research. Understanding patterns of herbivory across different habitats is important to understanding the dynamics of macroalgae and plant species throughout this marine ecosystem.

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A comparison of herbivory rates in an algae and seagrass bed in the west back reef of Discovery Bay, Jamaica

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Abstract: In reef flats, a variety of food resources are available to fish and urchin herbivores. Herbivores may prefer some foods or foraging habitats based on differences in nutritional quality, availability, accessibility, and proximity to cover of the food resource, as well as their vulnerability to predators while feeding on the food. In Discovery Bay, Jamaica, algae and seagrass food resources appear to differ primarily in nutritional quality. Seagrass (*Thalassia testudimum*) plant material is itself indigestible, although herbivores feed on the epiphytes growing on the blades. Therefore, despite possible morphological and chemical defenses which may be employed to deter herbivores, macroalgae (*Dictyota linearis* and *Amphiroa fragilissima*) may be a more easily digested and assimilated food resource. Thus, we would expect more foraging activity in algae than in seagrass habitats. We found a trend towards higher herbivory rates, and inferred higher herbivore abundance in the algae bed than in the seagrass bed ($p = 0.17$). We believe that this trend reflects the relatively high quality of algae as a food source. Alternatively, there may be no difference between herbivore abundance in the seagrass bed and the algae bed. Herbivores may have a mixed diet composed of seagrass epiphytes and macroalgae in order to maximize the benefits of both of these food resources.

Key Words: Amphiroa fragilissima, Diadema antillarum, Dictyota linearis, Thalassia testudimum, *macroalgal defenses, coral reef ecology*

Introduction

There are a variety of food resources available to herbivorous fish and urchins within the reef environment, including many types of algae and seagrass. Although herbivore diets are most likely composed of a number of different plant materials, they may feed more on one food than another based on its nutritional quality, availability, accessibility, proximity to cover, and their vulnerability to predators while feeding.

On the northern shore of Jamaica, in Discovery Bay, it appears that differences between algae and seagrass food resources lie primarily in nutritional quality. No herbivores, other than turtles, are able to digest the seagrass (*Thalassia testudimum*) plant material itself. Instead, fish and *Diadema antillarum* urchins selectively feed on epiphytes growing on the blades (Lobel and Ogden 1981). Despite possible morphological and chemical defenses, which may be employed to deter herbivores, macroalgae (*Dictyota linearis* and *Amphiroa fragilissima*) may be a more easily digested and assimilated food for fish and *D. antillarum* herbivores. If algae is a better food resource for herbivores, we would expect that more herbivores forage in algae beds compared to seagrass beds. If herbivory, or amount of a plant eaten, is a measure of herbivore abundance, then a higher amount of herbivory indicates more herbivores present in a particular habitat.

Methods

To compare herbivory rates between an algae and seagrass bed, we experimentally set seagrass blades in algae and seagrass beds within the west back reef of Discovery Bay, Jamaica, West Indies. The algae bed, which was composed of several macroalgae species including *Dictyota linearis* and *Amphiroa fragilissima*, covered an area of approximately 1600 m^2, and the adjacent seagrass bed covered an area of approximately 3000 m^2. These beds extended between 20 m from the shore

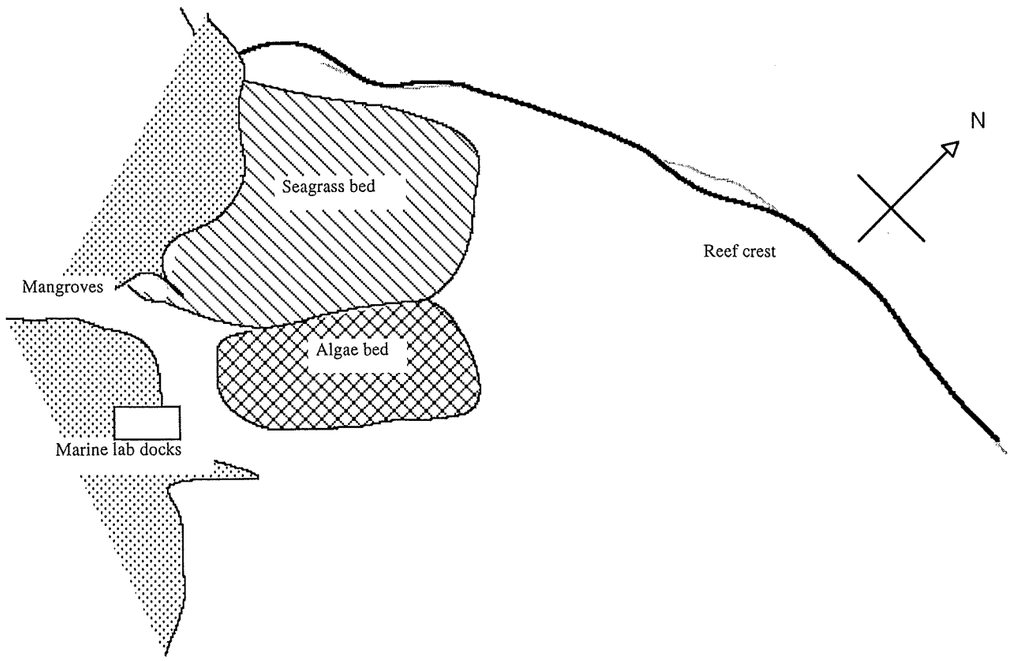

Figure 1. Seagrass bed and algae bed sites used to test herbivore abundance in Discovery Bay, Jamaica. Seagrass bed is approximately 3000 m^2; algae bed is approximately 1600 m^2.

in front of the Discovery Bay Marine Laboratory to the reef crest (Fig. 1).

Within each habitat we placed five replicates of ten uneaten seagrass blades that were held in place by two clothespins tied to a bolt and flagged with a scintillation vile buoy. Each seagrass blade was cut to 10 cm from the blade tip. All replicates were spaced greater than 10 m apart, and placed greater than 2 m from the edge of the algae or seagrass bed. Replicates were set in the bay on 26 February 2000 at 14:00 and collected 24 h later. The rate of herbivory was estimated as percent area lost per blade per 24 h, and averaged for each replicate. We compared treatments using a Kruskal-Wallis test.

Results

Although non-significant, there was a trend towards higher rates of herbivory on

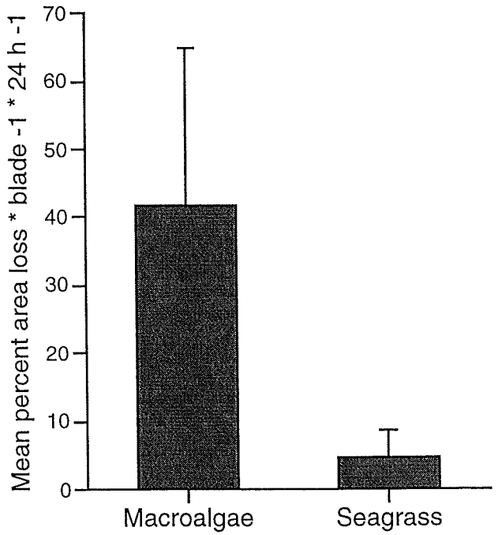

Figure 2. Average rate of herbivory (± SE) on seagrass blades (n = 5, 10 blades per replicate) in two vegetational habitats within the back reef at Discovery Bay, Jamaica

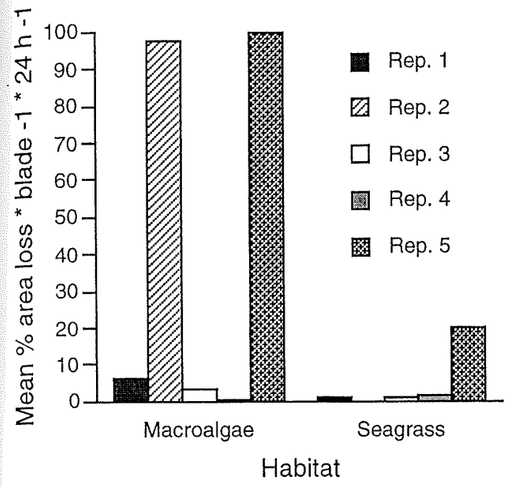

Figure 3. Average rate of herbivory on seagrass blades in each replicate (Rep.) (n = 10 blades per replicate) in two vegetational habitats within the back reef at Discovery Bay, Jamaica.

seagrass replicates in the algae bed compared to those in the seagrass bed (Fig. 2; $X^2 = 1.85$, df = 1, p = 0.17). Two replicates in the algae bed had between a 97% and 100% area loss for all blades, while the other three replicates ranged from 0.5% to 6.5% of the blade lost. One blade in the seagrass treatment had a 20% area loss to herbivory, and the other four replicates had between a 0% and 1.5% area loss (Fig. 3). Five blades in one of the seagrass replicates had been removed entirely from the clothespin at the time of collection and were not included in the analysis.

Discussion

The trend of higher herbivory in the algae bed than in the seagrass bed suggests a greater abundance of herbivores or grater foraging activity algae compared to seagrass beds. The digestibility of algae as compared to seagrass may be greater, providing a better source of nutrients in herbivore diets. However, algae may rapidly alter levels of morphological and chemical defenses with rate of herbivory (Paul and Van Alstyne 1992). Seagrass, on the other hand, represents a food resource of a constant quality. The relative benefits of foraging in seagrass and algae beds may therefore change over time with herbivory rates and concurrent changes in macroalgal defenses. Loss of large herbivores, due to decades of overfishing and a 1983 mass mortality of *Diadema antillarum* populations in Jamaican reefs (Lessios 1998), may have led to an overall reduction in macroalgal defenses, and therefore may partly explain the higher rate of herbivory found in algae beds compared to seagrass beds.

In spite of the trend of higher herbivory in algae beds, there was no statistical difference between the rates of herbivory in the two habitats, due to the high variability among replicates within habitats. We offer two explanations for these results. First, there may be no difference in the foraging rates between habitats. This lack of difference may be due to the absence of herbivore preference for algae or seagrass, resulting in a mixed diet. Herbivores may feed equally on seagrass epiphytes and macroalgae in order to maximize the benefits of both of these food resources. Second, the trend towards a higher rate of herbivory in the algae bed may simply be an artifact of density dependent foraging by fish (Rutar et al. 1997). Herbivores may be selecting the less dense and therefore more noticeable seagrass replicates in the algae bed. Repeating a similar study with algae replicates in algae and seagrass beds may conclusively eliminate the possibility of density dependent foraging and indicate differences in herbivore abundances between these two habitats.

The loss of large herbivores in this system has probably reduced competition for food resources among the remaining small herbivores, so that neither algae nor seagrass is limiting. Therefore, herbivores may be optimally feeding on the most nutritious diet composed of both the more easily assimilated

algae and epiphytes from seagrass blades. As the population of *D. antillarum* recovers and if fishing management practices curb overfishing, the re-establishment of large herbivores is likely to dramatically affect resource partitioning among large and small herbivores in reef flats.

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